

## Living in a physical world V. Maintaining temperature

STEVEN VOGEL

Department of Biology, Duke University, Durham, NC 27708-0338, USA

(Fax, 919-660-7293; Email, [svogel@duke.edu](mailto:svogel@duke.edu))

### 1. Introduction

Little else in our immediate world varies as much as the thermal loads that we terrestrial organisms face. Too often we find ourselves too hot, too cold, too well illuminated by sunlight, too exposed to an open sky, or in too great contact with hot or cold solid or liquid substrata. Thermal loads vary in time scale as well as in magnitude. Air temperatures and radiative regimes change over every time scale relevant to their operation, from seconds to years, at the least; in addition both soil and water temperatures may be far from constant. Variation may be as regular as night following day or it may be predictable only in a general statistical sense. Terrestrial life – and sometimes even aquatic life – is rife with thermal challenges.

The last essay (Vogel 2005) argued that variable internal temperature could impose serious constraints on biological design. It looked first at the way temperature, both extremes and fluctuations, might affect the operation of organisms. It then turned to the various physical agencies that could move heat to, from, and within organism. Here I will take a complementary look at these same issues, exploring the ways in which organisms can mitigate those fluctuations, focusing for the most part on how creatures can avoid moving heat.

Ideally, holding internal temperature at a value different from that outside should cost no energy – in general, all cost reflects imperfect thermal isolation. We might venture a sweeping generalization, asserting that adaptations for maintaining appropriate temperatures in a world of extremes and fluctuations have a particular common character. All (or, to be on the safe side, almost all) work by minimizing the metabolic work expended on temperature control. While energy economy may not be the transcendent issue that many of us once presumed, its importance cannot be denied.

And we might assert another generalization, a bit less sweeping than the preceding. Conduction, whether through air, water, or tissue, most often establishes a base line; pure conduction represents a kind of gold standard. For transfer within an organism, the central challenge comes down to reducing the convective heat transfer accompanying flow in blood vessels and air passageways to a level at which conduction predominates. If that can be done, avoiding excessive temperature fluctuations with minimum energy expenditure can take advantage of the conveniently low thermal conductivities of life's two main media, air and water – or, much the same as the latter, flesh and bone.

Thus air and water set the standards. All gases have low thermal conductivities; air's value,  $0.024 \text{ W m}^{-1} \text{ K}^{-1}$ , is ordinary for a gas or gas mixture – argon may be 32% and  $\text{CO}_2$  36% lower, but hydrogen is 7 times higher. Liquid water, at  $0.59 \text{ W m}^{-1} \text{ K}^{-1}$ , is quite as ordinary, here by comparison with other non-metallic liquids as well as solids – 40% lower than glass and 46% lower than limestone but about three times higher than pure fat, isolated whale or seal blubber (see Dunkin *et al* 2005), and common plastics such as the acrylics. Except, perhaps, for switching from watery muscle to minimally hydrated fat, reduction of thermal conductivity has little to offer.

(It should be noted that instead of thermal conductivity, animal physiologists often use thermal conductance, the combined rates of conductive and convective transfer per unit surface and per degree. With units of  $\text{W m}^{-2} \text{ K}^{-1}$  rather than  $\text{W m}^{-1} \text{ K}^{-1}$ , it ignores the thickness of any insulating layer. That makes good sense when looking at experimental data from irregularly shaped and variably coated animals. By contrast, data for conductivity usually comes from *in vitro* measurements on pelts and tissue samples. Thus finding that thermal conductance varies

inversely with thickness implies that thermal conductivity does not change.)

## 2. Circumventing convection

Air ordinarily moves unless prevented by some specific device, and it moves at speeds that matter. Speeds far less than our perceptual threshold of about  $0.5 \text{ m s}^{-1}$  still have thermal consequences. An oak leaf in the sun whose axial temperature at  $0$  to  $0.01 \text{ m s}^{-1}$  is  $41^\circ\text{C}$  will reach only  $37^\circ$  at  $0.1 \text{ m s}^{-1}$  (Vogel 1968). So “still air” in the meteorological sense may be presumed non-existent in the thermal world of organisms. If nothing else, any organism whose surface temperature differs from the surrounding air will experience self-induced free convection. Additionally, macroscopic organisms move fluids internally since some form of bulk transport is a practical prerequisite for getting much above cellular size. Such transport systems will move heat as well as material, and that heat transfer may have either positive or negative consequences.

One way to reduce internal convective heat transfer consists of simply reducing blood flow to the periphery and extremities by vasoconstriction. Small adjustments in relative vessel diameters can substantially reroute blood. We certainly do just that when inactive and exposed to cold, allowing our skin and appendages to stay at temperatures well below those of our brains and viscera. In the cold, it is normal for skin temperature to be  $10^\circ$  below that of the body's core. In one old experiment (DuBois 1939) nude males were asked to rest quietly in what was described as still air. Exposure to an ambient  $22.5^\circ\text{C}$ , perceived under the circumstances as quite chilly, dropped core temperature by about  $0.5^\circ\text{C}$ ; it dropped average skin temperature by  $7^\circ\text{C}$  – hands somewhat less, feet by as much as  $10^\circ\text{C}$ . In more extreme cold exposure we begin to defend core temperature by increased metabolic activity, noticeable as the minimally-coordinated muscular contractions of shivering, rather than by further reduction in peripheral circulation. These responses appear fairly general among warm-blooded vertebrates, not just unfurry and unfatty ones such as ourselves.

In practice, vasoconstriction combines two physical agencies. It reduces convection by creating a peripheral region in which flow is minimal. And it lowers conduction because lengthening the distance between central and surface temperature in, say, an appendage reduces the steepness of the temperature gradient. Experimental studies rarely tease apart the mix; one presumes that it varies case to case and place to place.

Adding insulation works in much the same way as vasoconstriction, again through a pair of physical agencies. And it has two biological manifestations – internal insulation using peripheral layers of fat and external insulation of fur and feathers.

Fat, as noted earlier, has an agreeably low thermal conductivity, about three times lower than water or meat. In addition, few tissues approach the low metabolic activity of subcutaneous fat – the reason metabolic rates are often referred to “lean body mass” for comparisons among different animals. Thus addition of subcutaneous fat reduces peripheral circulation as well. And subcutaneous fat layers can be remarkably thick, getting up to about 50% of total body volume in aquatic mammals that swim in cold waters. With this blubber, a seal can have both a skin temperature about a degree above  $0^\circ$  and a core temperature in the mid 30's (Irving and Hart 1957). The significant insulating effect of subcutaneous fat in humans underlies the common observation that females, with thicker layers, tolerate full-body exposure to cold water better than do males, whether they are Korean pearl divers or (at least as I have observed) marine biologists.

Fur and feathers permit effective conductivities to approach the value of pure air by limiting both free and forced convection. In no case does their own conductivity, that of the protein keratin, take on particular importance. Again we lack good data on how much of their effectiveness represents restriction of flow (usually air, in this case) and how much comes from reduction in the thermal gradient over which conduction occurs. Another uncertainty concerns the effects of ambient wind. Designing a fur coat of greatest effectiveness for its cost and thickness should depend on the importance of the free convection of the warm animal itself relative to that of environmental air movement. A fur coat has a dynamic component as well. Piloerection permits some degree of adjustment of its thickness and thus its thermal effectiveness – although our own attempts, noticed as so-called goose-flesh or goose-bumps (reminiscent of plucked poultry) accomplish little.

In practical terms (sweeping such complications aside) a single number provides a simple measure of the effectiveness of the fur coat of a mammal, given the near-uniformity of mammalian core temperatures and our consistent preference for insulation over metabolic increase. One needs only the temperature below which insulation is insufficient to permit a mammal to maintain normal eutherian body temperature at basal metabolic rate, the temperature below which metabolites must be expended simply to stay warm. Naked human males (females, with more subcutaneous fat, do a bit better despite their smaller sizes) have to turn up the fire at about  $27^\circ\text{C}$ , which is not at all impressive – presumably we are still warm-country pursuit predators, better adapted for heat dissipation than for conservation. Sloths do still worse, with critical temperatures around  $29^\circ\text{C}$ . Even small mammals, with fur length limited by other considerations, can do better, with weasels at  $17^\circ\text{C}$  and ground squirrels at  $8^\circ\text{C}$ . Large mammals, especially arctic ones

tolerate cold with remarkable economy – lower critical temperatures commonly run between 0°C and –40°C. (Scholander *et al* 1950).

### 3. Offsetting convection with countercurrent exchangers

A convective link between hot and cold locations need not transfer heat. The agency can be turned against itself – if it can carry heat one way, it should be able to carry it in the other quite as well. In the context of a warm animal in a cold place, the trick consists of transferring heat from blood flowing peripherally, not to the environment, but to blood flowing axially. The engineering literature refers to the device for doing that as a counterflow exchanger, physiologists prefer the word ‘countercurrent’ (often spelled ‘counter-current’). The key element is a region, typically near the base of an appendage, in which arteries and veins lie in sufficiently intimate juxtaposition for that heat transfer. If blood were to travel in the same direction in both arteries and veins, the best that could be achieved would be an output that averaged hot and cold inputs. But a counterflow arrangement, as in figure 1a, runs into no fundamental limit on transfer; practical limits are set by the intimacy of the vessels, flow rates, the conductivity of blood and vessel walls, and the outer insulation of the exchanger. Exchange is not limited to heat – diffusion, again, follows the same rules as conduction – and countercurrent exchangers conserve such substances as dissolved oxygen and water.

Figure 1b shows a device with which students in a course I once taught explored the operation of such exchangers. In practice they were asked to compare two, a countercurrent one in which flows ran in opposite directions (as in the figure) and one in which reversing a pair of connections made flows run concurrently. We quantified their deficiencies as the difference in temperature between input ( $T_{in}$ ) and output ( $T_{out}$ ) divided by the overall temperature difference between hot and cold ends ( $\Delta T$ ); subtraction from unity expressed data as exchange efficiency,  $e_e$ :

$$e_e = 1 - \frac{T_{out} - T_{in}}{\Delta T}. \quad (1)$$

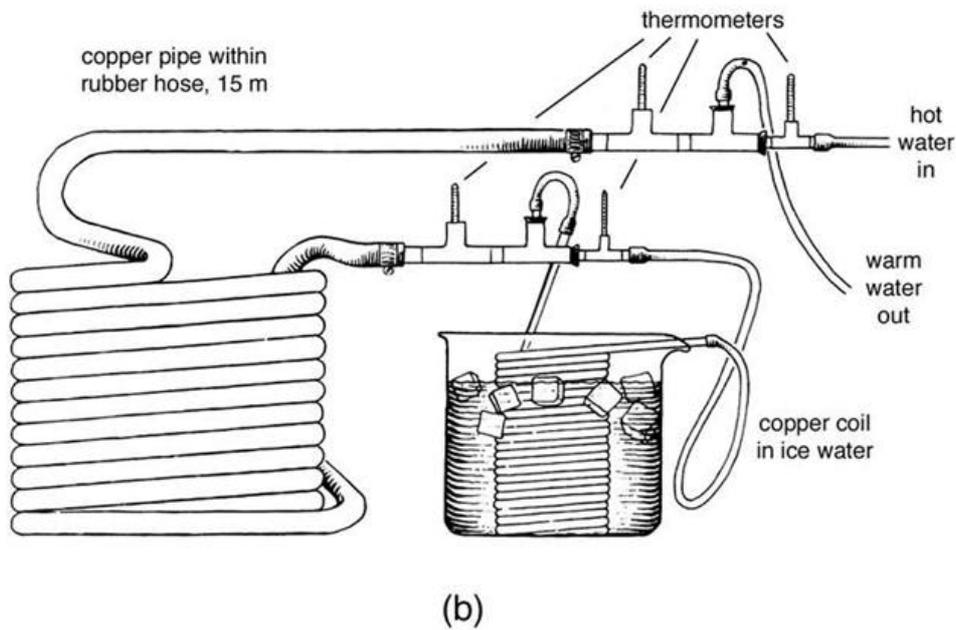
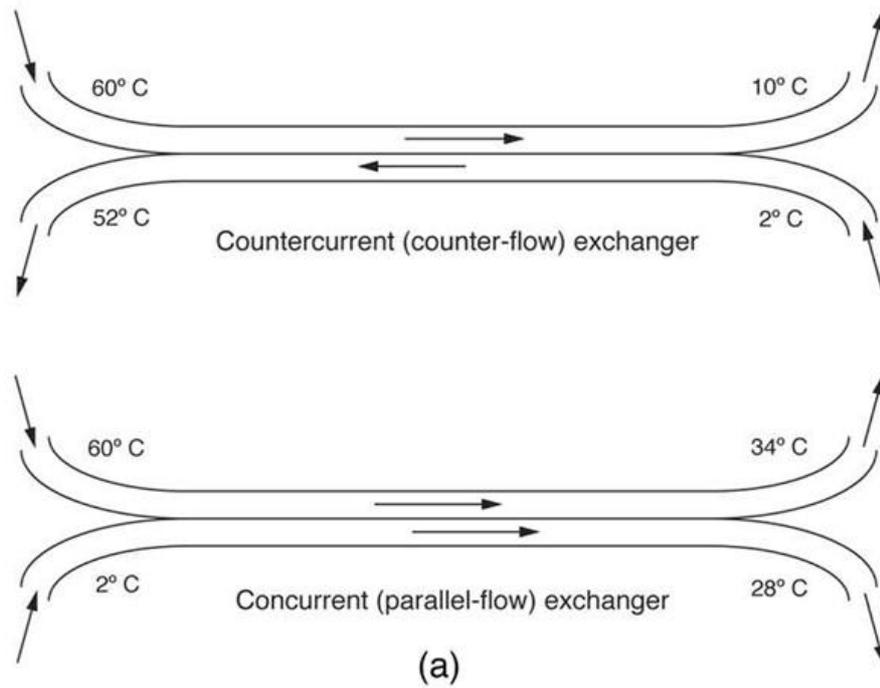
For both, plots of efficiency against flow speed showed that, as expected, faster flow reduced the effectiveness of exchange while slower flow gave better performance. But as flow speed decreased, the concurrent exchanger never quite reached 50% efficiency while, even this crude countercurrent device often exceeded 90%.

The recognition of countercurrent exchangers in organisms has a curious and instructive history. That the large arteries and veins of our appendages commonly lie close

together had been recognized for over three centuries before the suggestion, by the father of physiology, Claude Bernard, in 1876, that the combination might function as a heat exchanger. And early anatomists noted the wide distribution among other animals of local arrays of vessels branched to form, in cross section, networks of intermingled arteries and veins. They called such a structure a “rete mirabile” (plural ‘retia’), literally a “wonderful net”, or a “red gland” for the colour imparted by all that blood. Among others, Francesco Redi (1626–1697), still remembered for his experimental evidence against the spontaneous generation of maggots from meat, recognized retia. J S Haldane (father of the more flamboyant J B S Haldane) in his classic book, *Respiration* (1922), had the right idea about the fish swimbladder rete (an exchanger of dissolved gas, not heat). He drew an analogy with “a regenerating furnace, where the heat carried away in the waste gases is utilized to heat the incoming air”.

Somehow the common function of these retia escaped notice. Why? Traditional anatomists did not think in either functional or non-biological terms. Physiologists, with only rare exceptions until recently, focused on particular functions and particular animals, mainly humans, who happen to lack blatant examples of such exchangers. Take your pick of explanations. But once someone drew sufficient attention to the basic function of a rete, practically every known instance was quickly reexamined and assigned a functional role. Variants appeared, as did exchangers of less definitive anatomical character and less efficient operation. For instance, two veins (venae comitantes) surround the brachial artery of our upper arms, forming the exchanger noted by Bernard. The trio develops a lengthwise thermal gradient, though, of only about  $0.3^\circ\text{C cm}^{-1}$ , and we conserve more heat by shunting blood away from superficial vessels (Bazett *et al* 1948) than by its action.

Retia, then, have long been known; how they worked as countercurrent exchangers that could conserve either heat or diffusible molecules was first brought to general attention (one wonders whether the word ‘discovered’ applies) by an especially creative physiologist, Per Scholander (1905–1980) in the 1950’s. He credited Haldane, who credited Redi and others. His 1957 article in *Scientific American* seems to have provided that catalyst for the transition from obscurity to fashion. The first formally described function was not heat exchange but transferring dissolved gas in the vessels supplying the swimbladder of deep sea fish (harkening back to Haldane); the device allowed them to secrete and maintain gas in the bladder, gas that pressures of up to several hundred atmospheres should return to the blood, gills, and then ocean (Scholander and Van Dam 1954). The flukes and tail fins of small whales provided the first definitive



**Figure 1.** (a) Two heat exchangers, one in which fluid in the two channels flows in opposite direction and another in which it moves in the same direction. The temperatures represent typical results obtained by students using the device below. (b) A device that can be used as either a countercurrent (as here) or a concurrent exchanger. It consists of axial and annular channels and is made of ordinary flexible copper household plumbing, about 1.5 cm in diameter, rubber automotive heater hose, about 3 cm in diameter, copper plumbing fittings, and laboratory stoppers, thermometers, and tubing.

examples of heat exchangers (Scholander and Schevill 1955). Blubber, noted earlier, provides superb insulation, but thickly coated appendages would be ineffective as propulsors. Exchangers allow these animals to supply effectively cold-blooded fins with blood from an otherwise warm-blooded body and to do so without a futile investment of metabolic energy in heating the global ocean.

Highly effective countercurrent heat exchangers have now been described in the bases of the appendages of sloths, anteaters and some lemurs (Scholander and Krog 1957), the legs of wading birds (Scholander 1955; Kilgore and Schmidt-Nielsen 1975), the tails of muskrats (Irving and Krog 1955; Fish 1979), beavers, and manatees (Rommel and Caplan 2003), the legs of leatherback turtles (Greer *et al* 1973), the testicular blood supply of marsupials, sheep (Barnett *et al* 1958), bulls (Glad Sorensen *et al* 1991), and dolphins (Rommel *et al* 1992). They isolate the warm, dark, lateral muscles of large, fast-swimming tuna and mako sharks from the colder water passing along the body and across the gills (Carey and Teal 1966, 1969; Dewar *et al* 1994). Gazelles, sheep, and some other ungulates keep their brains from getting as hot as the rest of their heat-stressed bodies with a carotid rete, in which ascending arterial blood is cooled by venous blood coming from evaporatively cooled nasal passages (Baker and Hayward 1968). Honeybees and some other Hymenoptera isolate their abdomens from their hotter thoraces in flight with exchangers in their narrow, wasp-waist petioles (Heinrich 1996). Most of these exchangers can be bypassed by opening shunting vessels, so an animal can use an appendage as a heat dissipation device when (usually during locomotion) needed.

All the preceding countercurrent exchangers operate as steady-state devices. Unsteady versions that briefly store heat occur in both mammals and birds as well, again a scheme whose wide use was evident only after recognition of the first. Here the nasal passages of a North American desert rodent, the kangaroo rat, provided the initial case. Jackson and Schmidt-Nielsen (1964) showed that during exhalation heat moved from the air stream to the walls of the passages, so air left an animal near – in a dry atmosphere slightly below – ambient rather than body temperature. During inhalation, heat moved from passage walls to air, warming it and cooling the walls. In desert rodents its primary function appears to be water conservation, with over 50% of respiratory water loss (their principal mode of leakage) avoided by this condensation during exhalation and reevaporation during inhalation. But they economize on heat as well, in amounts significant relative to overall metabolic rates, recapturing over 60% of the energy used to heat and humidify inhaled air (Schmidt-Nielsen 1972). Camels use their enormously surface-endowed nasal turbinates in the same manner; for them,

concomitant thermal economizing may be detrimental rather than advantageous (Schmidt-Nielsen 1981).

Both children and adult humans exhale air close to core temperature. I wonder, though, about neonatal humans. My son, when about a week old (a smaller-than-average baby who is now a larger-than-average adult), seemed to be exhaling air that was quite a lot cooler than what came out of my own nose.

#### 4. Buffering fluctuations through short term storage

We may be less immediately aware of the problems of temperature variation than of inopportune temperature *per se*. Our large size buffers us from changes in ambient temperature and radiant regime, and our mobility usually enables us to quickly reach more salubrious locations. Our perceptual world remains distant from that of a marine snail caught on a large rock in summer sunlight at low tide or of a sun-lit leaf on a tree when the normally ubiquitous air movements briefly abate. But, as Denny and Gaines (2000) remind us, the distribution of organisms more likely reflects local extremes, particularly temporal ones, than it does regional averages.

What constitutes a temporal extreme, though, depends on size. As large creatures we can ignore most events that last only seconds and need not take seriously most minute-scale phenomena. I can move a finger through a candle flame without discomfort, much less injury; and I recall watching students on a Canadian campus going without coats from one building to an adjacent one despite a temperature of about –30°C. At the same time, few, even well bundled, waited in the open for buses. So we encounter yet another problem of scale, that ever-lurking consideration in each of these essays.

While minute-to-minute fluctuations in heat load may not matter to large animals, variation on scales of hours clearly do. A particularly interesting case is that of a camel in a hot desert, faced with problems of both too much heat and too little water, something investigated by Schmidt-Nielsen *et al* (1957) and later put into a general context (Schmidt-Nielsen 1964). Comparison of normal and shorn animals showed that fur reduces both heat gain and evaporative water loss. Beyond using fur, camels (dromedaries in North Africa) take peculiar advantage of the predictability of the main temporal fluctuation that affects them. When their access to water is limited, they permit their core temperatures to rise from about 34°C to 40°C during the day, secure in the knowledge that night will follow with cooler air and (usually) an open sky. They thereby reduce evaporative water loss (less sweating, mainly) almost three-fold and halve overall water loss.

One might expect that only large creatures can play this particular game – a few large mammals, perhaps some

of the more massive cacti (Nobel 1999 calculated time constants for the latter of several hours). Remarkably, at least one group of small desert succulents heats slowly enough to do so as well. These so-called stone plants (*Lithops* spp.) live largely buried in the soil of the Namib desert and the Karoo scrubland of South Africa; they protrude only about 2 mm above the surface but extend downward about 30 mm, as in figure 2. A translucent window on the top of each of the paired leaf-analogs admits light into the interior, with the photosynthetic tissue (the chlorenchyma) lining the bottom somewhat as our retinas line the inner rear surface of our eyeballs. Turner and Picker (1993) found that daily temperature cycled between extremes of 12°C and 46°C, as very nearly did plant surface, plant interior, and the surrounding soil 1 cm below the surface – all rose rapidly though the morning, peaked in the afternoon, and slowly dropped through the night. That may be more variation than experienced by a camel, but direct solar exposure without coupling to the surrounding soil would make matters worse – plants surrounded by styrofoam insulation became considerably hotter than those in full contact with the soil.

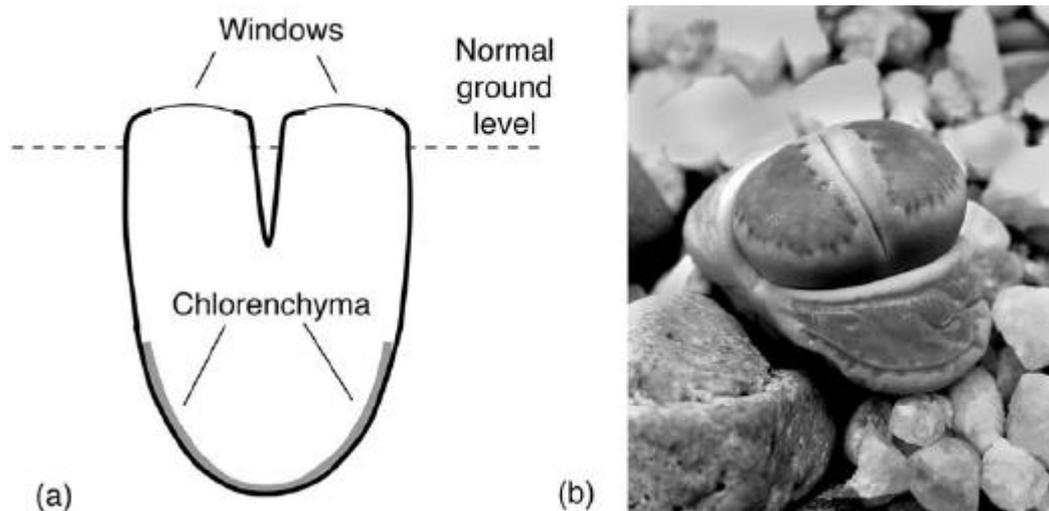
Thus by combining its thermal mass with that of the surrounding soil, *Lithops* buffers its daily temperature changes and, most importantly, reduces peak daytime temperatures. In addition, it takes advantage of the steep vertical thermal gradient in the soil, coupling not to the hotter surface but to the cooler soil a short distance beneath and by locating its most metabolically active tissues well down from that hot surface.

To emphasize the connection between the size of the system and the relevant temporal scale of fluctuations we

might return to broad leaves during periods of what we think of as still air. Convection, whose magnitude depends strongly on air speed, provides a major avenue of heat transfer. The speed of “still air” fluctuates rapidly and continuously, the result of passing turbulent structures and local convection. And leaves, with lots of surface and little volume, are effectively small and thus have very rapid thermal responses.

Some years ago I tried to get a sense of a leaf’s thermal situation on a still, sunny summer afternoon with a model leaf mounted near the top of the forest canopy. The model, of cellulose acetate with black ink dots, had both the shape and thickness of a sun leaf of white oak (*Quercus alba*) – testing in the laboratory assured me that its absorptivity and time constant came close to those of real leaves. A tiny bead thermistor glued to its lower surface monitored mid-blade temperature, while a heated thermistor tracked adjacent air movement. Figure 3 shows a typical pair of tracks. Air temperature remained almost constant, and model temperature invariably exceeded it. The temperature of the leaf model was anything but constant; when the wind dropped, it rose, with only a short lag. One rarely, if ever, thinks of leaf temperature as such a wildly fluctuating variable; once alerted, one wonders about the metabolic implications of its rapid and continuous change.

Nobel (1999) calculated a time constant below 20 s for a broad leaf, quite consistent with the data from my model in figure 3. As one can see from that figure, even a modest increase in such a time constant would yield significant thermal buffering, so rapidly does air speed change. Thus improved protection against temperature extremes would require vastly less mass than a camel or



**Figure 2.** (a) Diagrammatic cross section of a mature *Lithops*. (b) *Lithops*, as grown in a greenhouse and less deeply buried than it would be in nature. The above-ground portion is about 2 cm across.

stone-plant-plus-soil. And thus increased thickness might well constitute a specific adaptation to assure lower peak temperatures during brief episodes of especially low wind – as opposed to an incidental consequence of some other functional demand. Plants with small, thick leaves have long been termed ‘xerophytes’ for their prevalence in dry habitats; the leaf structure is then ‘xeromorphic’. Perhaps the plants might instead be called ‘thermophytes’, the lack of local water for evaporative cooling simply contributing to the thermal challenge they face.

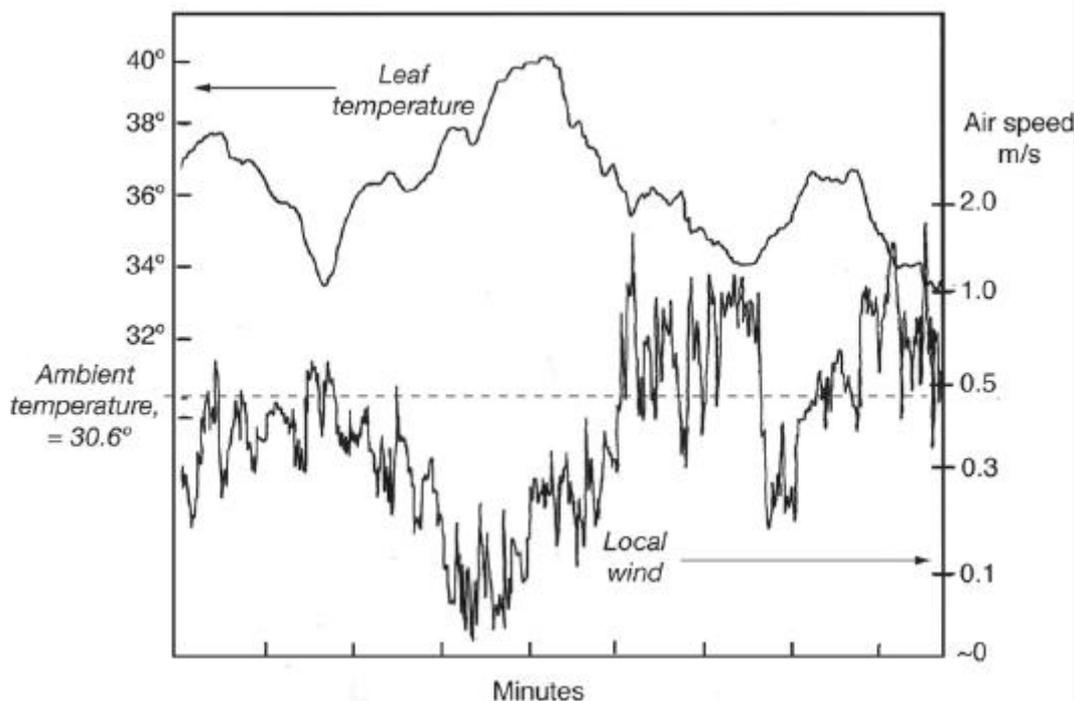
A functional explanation that focuses primarily on heat and only secondarily on water might explain the peculiar prevalence of plants with xeromorphic leaves in some well-watered places such as the swampy bogs of eastern North America. Traditional explanations invoke some kind of physiological dryness or deficiencies of nitrogen or calcium. But the results of a comparative morphological study by Philpott (1956) are consistent with a thermal rationale. She matched leaves of 19 species from forest-surrounded bogs in Carolina (called ‘pocosins’ in the region) with those of 14 related plants from the Appalachian mountains directly inland. Whether looking at specific genera or at averages, the bog plants had smaller and thicker leaves. Small size would give better convective coupling to the surrounding air and therefore less deviation from ambient temperature; thicker leaves would heat

more slowly during lulls. Thus the low wind and high humidity that makes these bogs notoriously unpleasant for people may be just the factors that challenge the local plants.

Somewhat more direct evidence that leaves may decrease size and increase thickness to lower peak temperatures through short term heat storage comes from work of Kincaid (1976). He collected holly (*Ilex*) leaves of a variety of species that experience different thermal extremes and exposed them to a wide variety of regimes in a very low speed wind tunnel in my laboratory. Among other manipulations, he subjected radiantly-heated leaves to pulses of moving air, alternating 10 s of still air ( $< 0.01 \text{ m s}^{-1}$ ) with 10 s of winds of  $0.1$  and  $0.5 \text{ m s}^{-1}$ , conditions of light and air movement that he showed were in a range they might normally encounter on a hot, windless day. Larger and thinner leaves heated significantly faster and further during lulls than did smaller and thicker ones. The variation in behaviour among the different species in the wind tunnel correlated satisfyingly with estimates of the importance of short term heat storage from field data.

### 5. The possibility of counterconvection

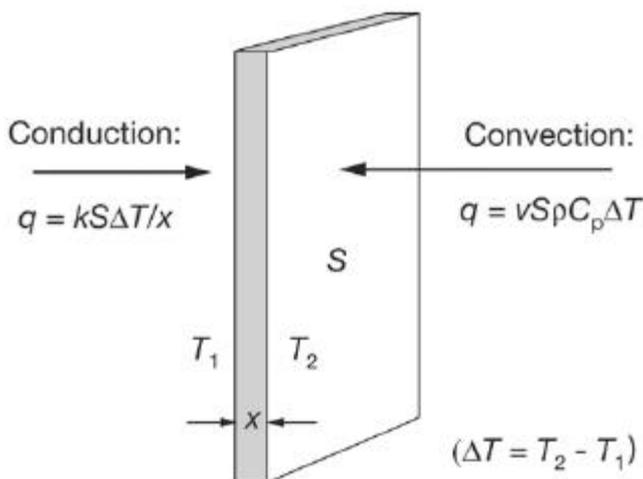
In examining how the physical world affects the adaptations and aspirations of organisms, this series of essays



**Figure 3.** Representative data for air temperature, mid-blade leaf temperature, and wind speed for a model sun leaf of white oak, *Quercus alba*, on a typically windless summer afternoon in the Carolina piedmont. Note the non-linear scale for wind speed.

attempts general perspectives rather than conventional reviews. I want to include in my domain physical devices as yet unknown in living systems – one can, as an alternative to our normal search for functional explanations of specific features of organisms, look for organisms that use some hypothetical but plausible device. Per Scholander's recognition of the commonness, diversity, and general function of biological countercurrent exchangers – as well as much else he did – certainly shows the utility of the approach. In a sense, he played Hamlet to us Horatios; as Shakespeare put it, "There are more things in heaven and earth, Horatio, than are dreamt of in your philosophy".

Consider a related scheme not yet known in a biological system. Countercurrent devices combine convective with conductive or diffusive transfer – fluid moves axially through pipes while heat or molecules conduct or diffuse laterally through the fluid and across the walls separating the pipes. These two modes of moving heat or molecules can be combined in another way, one that could permit heat transfer to be driven below what we have been treating as a baseline, pure conduction – achieving, in effect, perfect insulation. Credit for asking about its possible roles should go to an engineer, the late Lloyd Trefethen. He described the scheme and asked me whether it found use; I could offer no specific instance. Perhaps some reviewer or reader will recognize a case of what has been called 'counterconvection'. It operates in the following way – focusing on heat transfer, but bearing in mind that diffusive material transfer and a concentration gradient could replace heat conduction and a temperature gradient.



**Figure 4.** Heat conduction, left to right, and convection, right to left, in a counterconvective arrangement.  $S$  and  $x$  are slab area and thickness respectively,  $k$  is thermal conductivity,  $v$  is cross-slab flow speed,  $\rho$  is fluid density, and  $C_p$  is the heat capacity of the fluid.

Imagine a porous, conductive barrier between two compartments that differ in temperature, as in figure 4. Heat ought to be conducted from warmer to cooler side. That conduction, though, is exactly offset by fluid forced through the barrier, so that all the heat that would otherwise be conducted down the thermal gradient gets transferred to fluid flowing up that gradient. And fluid flowing up the thermal gradient, now preheated, no longer cools the warmer compartment as it enters. In effect, heat moves down a thermal gradient while fluid moves down a pressure gradient, with conduction in one direction balanced by convection in the other. Balance will be achieved when

$$\frac{k}{x} = v\rho C_p, \quad (2)$$

where  $k$  is thermal conductivity,  $x$  is the thickness of the barrier,  $v$  is flow speed,  $\rho$  is fluid density, and  $C_p$  is heat capacity (or specific heat at constant pressure).

The principal difficulty, to provoke proper skepticism at the start, is that the mechanism does not (at least as I see it) lend itself to operation as a closed cycle. Fluid will accumulate in one compartment, so draining it in any ordinary way will offset anything gained. Actively pumping fluid will leave the system still worse. This suggests examining systems where fluid ordinarily enters or leaves and can be secondarily pressed into counterconvective service or systems that operate only part time, perhaps during periods of particular environmental stress.

Does the possibility pass quantitative muster? Consider two cases in which hypothetical organisms find themselves in dangerously hot circumstances:

(i) A spherical animal with  $1 \text{ m}^2$  of outer surface (0.56 m in diameter) and an insulating layer of fat 0.01 m thick is exposed to an outside temperature  $10^\circ\text{C}$  above body temperature; high humidity or a liquid external medium prevents evaporative heat transfer. If fat's conductivity is  $0.21 \text{ W m}^{-1} \text{ K}^{-1}$ , Fourier's law for conduction predicts heat entry at 210 W. Expelling it in the form of water, with a heat capacity of  $4.2 \text{ kJ kg}^{-1} \text{ K}^{-1}$  would take only  $5 \text{ ml s}^{-1}$ . Still, that amounts to  $181 \text{ h}^{-1}$ , which would use up the entire volume of the animal in just a little over 5 h, making the scheme an unattractive long-term fix. That 210 watt heat entry would normally cause the animal to heat (initially at least) at about  $1.9 \text{ K h}^{-1}$ , which ought to be tolerable for short periods. So counterconvection would not work well for long periods and would be unnecessary for short periods. Still, the scheme cannot be dismissed as impossible for all scales of size, time, and temperature.

(ii) Another spherical animal of the same size and faced with the same temperature difference has no insulating fat; instead it has a fur coat of the same (0.01 m) thick-

ness. Heat conducts inward through the fur while perspired liquid water is wicked outward and then obligingly disappears with no additional thermal consequences. Conductivity is now  $0.025 \text{ W m}^{-1} \text{ K}^{-1}$ , and heat will enter at 25 W. That requires an outward flow of water of only  $0.6 \text{ ml s}^{-1}$  or  $2.15 \text{ l h}^{-1}$ . The animal thus contains about 44 h supply, enough, one might guess, to deal with a hot afternoon in the secure knowledge that night will follow in a few hours. But one further calculation puts this sanguine scenario in a less favourable light. Dealing with an input of 25 W by evaporative cooling, given water's heat of vaporization of  $2.44 \text{ MJ kg}^{-1}$ , would take only  $0.037 \text{ l h}^{-1}$ , about 60 times less. Thus the scheme, while possible, makes sense only where evaporative cooling cannot be relied upon.

What should we conclude? While we should not dismiss the possibility of counterconvection, the requirements for it to be worthwhile turn out to be daunting. Still, conduction through a material of low conductivity and flow through a porous barrier, the requirements for it to happen, are biologically ordinary. One can produce enough bulk flow through such a barrier with only a modest pressure gradient, and organisms often either absorb or excrete liquid water for other purposes at appropriate rates.

#### Acknowledgements

I thank Dwight Kincaid and Knut Schmidt-Nielsen for steering me to important sources of information and the Duke University greenhouse for access to *Lithops*. I remain indebted to the late Jane Philpott and Lloyd Trefethen for stimulating my interest in aspects of the present topic, and I treasure the memory of my brief encounters with Pete Scholander.

#### References

- Baker M A and Hayward J N 1968 The influence of the nasal mucosa and the carotid rete upon hypothalamic temperature in sheep; *J. Physiol., London* **198** 561–579
- Barnett C H, Harrison R J and Tomlinson J D W 1958 Variations in the venous system of mammals; *Biol. Rev.* **33** 442–487
- Bazett H C, Love L, Newton M, Eisenberg L, Day R and Forster R II 1948 Temperature changes in blood flowing in arteries and veins in man; *J. Appl. Physiol.* **1** 3–19
- Bernard, C 1876 *Leçons sur la chaleur animale, sur les effets de la chaleur et sur la fièvre* (Paris: J-B Baillière)
- Carey F G and Teal J M 1966 Heat conservation in tuna fish muscle; *Proc. Natl. Acad. Sci. USA* **56** 1464–1469
- Carey F G and Teal J M 1969 Mako and porbeagle: warm-bodied sharks; *Comp. Biochem. Physiol.* **28** 199–204
- Denny M and Gaines S 2000 *Chance in biology: Using probability to explore nature* (Princeton, NJ: Princeton University Press)
- Dewar H, Graham J B and Brill R W 1994 Studies of tropical tuna swimming performance in a large water tunnel. II. Thermoregulation; *J. Exp. Biol.* **192** 33–44
- DuBois E F 1939 Heat loss from the human body; *Bull. N.Y. Acad. Med.* **13** 143–173
- Dunkin R C, McLellen W A, Blum J E and Pabst D A 2005 The ontogenetic changes in the thermal properties of blubber from the Atlantic bottlenose dolphin *Tursiops truncatus*; *J. Exp. Biol.* **208** 1469–1480
- Fish F E 1979 Thermoregulation in the muskrat (*Ondatra zibethicus*): the use of regional heterothermia; *Comp. Biochem. Physiol.* **A64** 391–397
- Glad Sorensen H, Lambrechtsen J and Einer-Jensen N 1991 Efficiency of the counter current transfer of heat and  $^{133}\text{xenon}$  between the pampiniform plexus and testicular artery of the bull; *Int. J. Androl.* **14** 232–240
- Greer A E, Lazell J D and Wright R M 1973 Anatomical evidence for a countercurrent heat exchanger in the leatherback turtle (*Dermodochelys coriacea*); *Nature (London)* **244** 181
- Haldane J S 1922 *Respiration* (New Haven, CT: Yale University Press)
- Heinrich B 1996 *The thermal warriors: Strategies of insect survival* (Cambridge, MA: Harvard University Press)
- Irving L and Hart J S 1957 The metabolism and insulation of seals as bare-skinned mammals in cold water; *Can. J. Zool.* **35** 497–511
- Irving L and Krog J 1955 Temperature of the skin in the Arctic as a regulator of heat; *J. Appl. Physiol.* **7** 355–364
- Jackson D C and Schmidt-Nielsen K 1964 Countercurrent heat exchange in the respiratory passages; *Proc. Natl. Acad. Sci. USA* **51** 1192–2297
- Kilgore D L Jr and Schmidt-Nielsen K 1975 Heat loss from ducks' feet immersed in cold water; *Condor* **77** 475–478
- Kincaid D T 1976 *Theoretical and experimental investigations of Ilex pollen and leaves in relation to microhabitat in the southeastern United States*, Ph.D. Thesis, Wake Forest University, Winston-Salem, NC, USA
- Nobel P 1999 *Physicochemical and environmental plant physiology*, 2nd edition (San Diego, CA: Academic Press)
- Philpott J 1956 Blade tissue organization of foliage leaves of some Carolina shrub-bog species as compared with their Appalachian mountain affinities; *Bot. Gaz.* **118** 88–105
- Rommel S A and Caplan H 2003 Vascular adaptations for heat conservation in the tail of Florida manatees (*Trichechus manatus latirostris*); *J. Anat.* **202** 343–353
- Rommel S A, Pabst D A, McLellen W A and Potter C W 1992 Anatomical evidence for a countercurrent heat exchanger associated with dolphin testes; *Anat. Rec.* **232** 150–156
- Schmidt-Nielsen K 1964 *Desert animals: Physiological problems of heat and water* (Oxford, UK: Oxford University Press)
- Schmidt-Nielsen K 1972 *How animals work* (Cambridge, UK: Cambridge University Press)
- Schmidt-Nielsen K 1981 Countercurrent systems in animals; *Sci. Am.* **244** 118–129
- Schmidt-Nielsen K, Schmidt-Nielsen B, Jarnum S A and Houpt T R 1957 Body temperature of the camel and its relation to water economy; *Am. J. Physiol.* **188** 103–112
- Scholander P F 1955 Evolution of climatic adaptations in homeotherms; *Evolution* **9** 15–26
- Scholander P F 1957 The wonderful net; *Sci. Am.* **196** 96–107
- Scholander P F and Krog J 1957 Countercurrent heat exchange and vascular bundles in sloths; *J. Appl. Physiol.* **10** 405–411
- Scholander P F and Schevill W E 1955 Counter-current vascular heat exchange in the fins of whales; *J. Appl. Physiol.* **8** 279–282

- Scholander P F and Van Dam C L 1954 Secretion of gases against high pressures in the swimbladder of deep sea fishes; *Biol. Bull.* **107** 247–259
- Scholander P F, Walters V, Hock R and Irving L 1950 Heat regulation in some arctic and tropical mammals and birds; *Biol. Bull.* **99** 237–258
- Turner J S and Picker M D 1993 Thermal ecology of an embedded dwarf succulent from southern Africa (*Lithops* spp: Mesembryanthemaceae); *J. Arid Environ.* **24** 361–385
- Vogel S 1968 “Sun leaves” and “shade leaves”: differences in convective heat dissipation; *Ecology* **49** 1203–1204
- Vogel S 2005 Living in a physical world IV. Moving Heat Around; *J. Biosci.* **30** 449–460

ePublication: 22 November 2005